

Some Observations on Spatial Distribution in a Montane Population of *Euphydryas editha*

Paul R. Ehrlich

and

Darryl Wheye

Department of Biological Sciences, Stanford University, Stanford, CA 94305

Abstract. Counts of montane *Euphydryas editha* along transects at Almont Summit, Colorado, show that males form a dense aggregation along a ridgetop with an estimated 30:1 (male:female) sex ratio. Fertilized females showed preference for subsites below the ridgetop at least as rich in oviposition plants but less rich in nectar resources, where the sex ratio was close to 1:1. Mark-release-recapture data suggest mating is less probable on the ridgetop than below it. This suggests the possibility that non-aggregating males, at least under conditions similar to those of 1983, may have greater reproductive success than those in aggregations, raising questions about the function of such aggregations.

Recently it has been suggested that the availability of fertilizable females is the link between ecological factors and mating systems in butterflies (Odendaal et al., 1984). Several tentative hypotheses were advanced about the characteristics of mating systems in populations with short and long periods of female availability. The assumption was made that the duration of female availability in butterflies is largely determined by the length of the period in which the larvae will have access to suitable resources.

Odendaal et al. used Nearctic checkerspot butterflies of the genus *Euphydryas* (Nymphalidae: Nymphalinae) as exemplars of explosive breeders, since time for development of their larvae is, in general, severely limited by the growth cycle of their larval food plants. For such butterflies, Odendaal et al. predicted, among other things, (1) synchronization of female emergence so that their availability is short, (2) a strong tendency for males to form dense aggregations where the structure of the population is "open" (i.e., where resource or other constraints do not concentrate individuals in relatively restricted areas), (3) relatively little spatial overlap between males and fertilizable females, (4) an operational sex ratio (OSR) biased toward males in the mating area and (5) little

choosiness by males in selecting mates. We tested some of these hypotheses in a Colorado population of *Euphydryas editha* during the summer of 1983.

Materials and Methods

Near Almont, Gunnison County, Colorado, *E. editha* forms diffuse colonies between about 2700 and 3000 m in sagebrush-dominated meadows where the larval food plant, *Castilleja linariifolia*, a hemiparasite on sagebrush (*Artemisia*) and appropriate nectar resources are available (Ehrlich and White, 1980). A concentration of these butterflies at Almont Summit (2800-3000 m) has been under study since 1976 (Holdren and Ehrlich, 1982). To determine the distribution of the two sexes, we used mark-release-recapture (MRR) techniques (Ehrlich and Davidson, 1960; Brussard, 1971) and transect counts (see Pollard, 1977). A total of 3400 m of transects were established (Fig. 1). One 350 m transect followed a dirt road along a ridge at 3000 m, above a topographically diverse slope (Fig. 2). Other transects crisscrossed three benches cascading from the ridgetop and separated by steep slopes, unsuitable, or marginally suitable habitat.

The distributions of the larval host plant, *C. linariifolia* and various nectar resources were mapped. The latter included primarily *Senecio integerrimus* (the one on which most nectaring is observed regardless of the relative abundance of flowers), and secondarily *Erigeron* sp. early in the season, and, as the *Erigeron* senesced, *Wyethia amplexicaulus*. We also recorded the collective distribution of *Taraxacum officinale*; *Agoseris glauca*, another yellow composite; *Allium textile*; and *Pseudocymopterus montanus*; all of which were occasionally visited for nectar. To determine plant distributions, we estimated abundances along each 50 m segment on a scale of 0 (absent) to 3 (abundant). By averaging the estimated abundances of the 50 m segments comprising the ridgetop and three south-southeast facing benches fanning out below it, distributions were roughly evaluated in these four main areas where more than $\frac{3}{4}$ of the butterflies had concentrated (Table 1). Because all four areas include segments lacking abundant resources, none received an average rating of 3.

The transects were walked by both of us simultaneously in varying patterns and directions on 11 days between 23 June and 18 July. The 350 m transect along the road was walked eighteen times (once on six days, twice on four days and four times on one day), and other transects were walked on alternate visits. The counts for the less frequently walked transects were corrected by multiplication to the standard of the road transect (e.g., one walked nine times had its count doubled). Where *Euphydryas* were common, one of us observed while the other recorded. Effort was made to maintain a pace of 2 s/m, except where butterflies were very

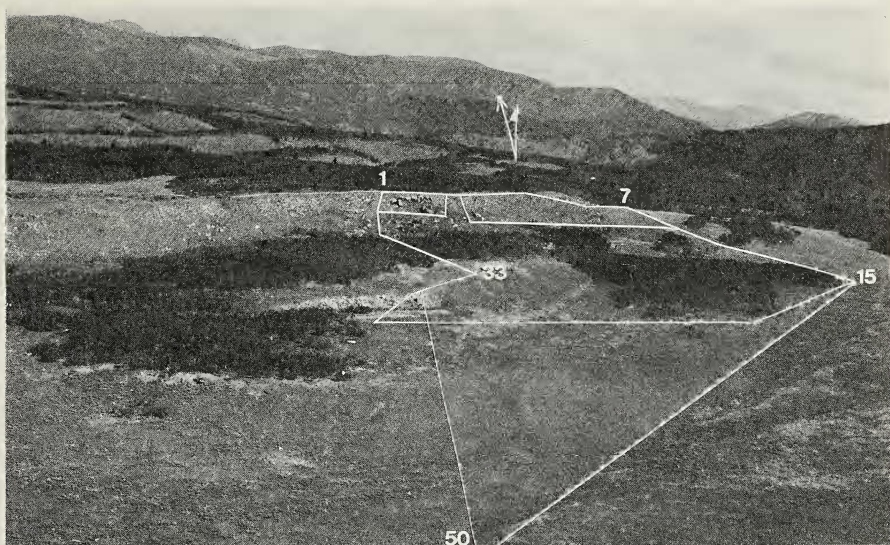


Fig. 1. Aerial photograph of Almont Summit, Gunnison Co., Colorado showing transects.

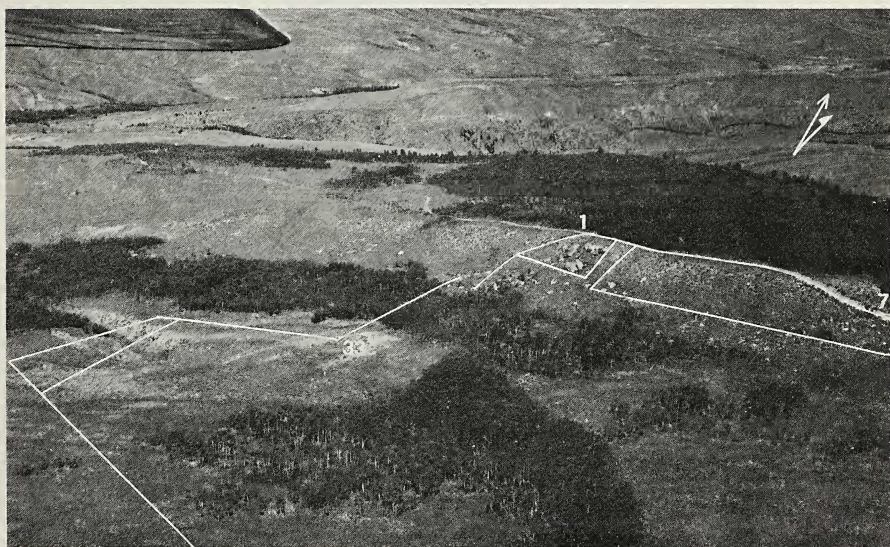


Fig. 2. Close-up aerial photograph of Almont Summit, Gunnison Co., Colorado, showing road and benches (33 is on first bench, second bench is at furthest left point on transect).

Table 1. Summary of *Euphydryas editha* (using corrected numbers), oviposition plant and nectar source distribution at Almont Summit, Colorado, determined during transect counts, June-July, 1983.

Site	TOTAL SEEN		% OF TOTAL		% OF SEX		RATIO Male:Female	FOOD* Plant	NECTAR* Resources
	Male	Female	Male	Female	Male	Female			
Road	543	18	.499	.017	.581	.117	29.5:1	2	2-2**
1st Bench	180	25	.165	.023	.192	.161	7.2:1	1	0-1
2nd Bench	11	14	.010	.013	.012	.092	.8:1	1	0-1
3rd Bench	81	69	.074	.063	.089	.444	1.2:1	2	0-1
Remaining Sections	118	30	.108	.028	.126	.186			
Total	933	156	.856	.144	1.000	1.000			

*0 = none seen

1 = plants scarce

2 = plants common

**First number refers to *Senecio integerrimus*

Second number refers to secondary nectar resources

scarce. In those areas the pace was roughly twice as fast, but the observations of both of us were recorded. In practice, this means *E. editha* were recorded if they were present within about 2.5 m on either side of the transect. For more than 99 percent of these sightings the sex was recorded as well.

In addition, during 7 visits to the site (between 2-18 July) a total of 167 male and 53 female butterflies caught along the transects were given individual marks using standard techniques and released. These marked butterflies were included in the transect counts.

Results

Both larval host plant and nectar resources are distributed over much of the area in the vicinity of the transects (Fig. 3). *Castilleja linariifolia* was

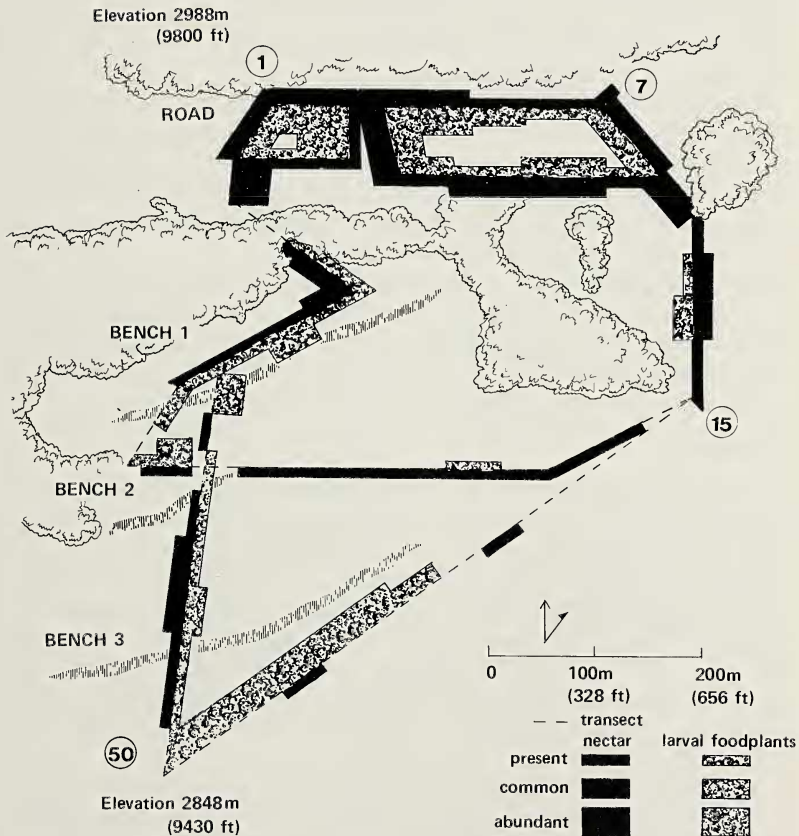


Fig. 3. Distribution of larval host plant and nectar resources along transect.

more common along the third bench than along the ridgetop, and more common on the ridgetop than on the first and second benches. Primary nectar resources were abundant along the ridgetop, scarce on the first bench, absent on the second, and scarce on the third. Similarly, secondary nectar resources were common along the road and less common to scarce along the benches (Table 1).

Distribution of the two sexes is shown on the map in Figure 4. The data presented in the figure accords well with our subjective evaluation of their relative abundance in different areas.

While individual *E. editha* could be seen throughout most of the area, Table 1 (using corrected numbers) lists the estimated distribution by sex and the ratio of males to females found in the four preferred areas. We found that males tended to form a dense aggregation along the ridgetop. During transect walks, an average of 29 individuals were seen along the 350 m ridgetop section compared with 22 individuals along the remaining 3050 m of transects criss-crossing the site. Females, in contrast, were found primarily on the third bench.

Recapture data confirmed male movement into but not out of the area of aggregation. During each walk of the ridgetop transect an average of 64% of the catch were first-time captures. Yet, of the 61 males recaptured there, 55% were caught within 50 meters of their original capture. Furthermore, of the 104 males marked in the ridgetop aggregation, none were later seen on the third bench.

Recapture data showed no female movement into or out of the area of male aggregation. We could not determine where most matings occurred, but we assumed larval hostplants on the third bench were preferred for oviposition, because 44% of the females seen during the transect walks (using the corrected numbers, see Table 1) were found there.

Discussion

That selection has favored synchrony of female availability in *Euphydryas* is indicated by the temporal patterns of oviposition. Females emerge with a large complement of eggs, and, at least in central California populations for most years, only larvae from the earliest two masses have the opportunity to develop to diapause. In addition, in laboratory experiments, the size of these early masses is unaffected by foraging prior to oviposition (Murphy, et al., 1983). The phenology of the oviposition plants in the montane population at Almont Summit (Holdren and Ehrlich, 1982) would also appear to place a premium on early emergence and oviposition.

Our results also indicate that female fitness depends upon the availability of oviposition plants in suitable condition, and that selection should favor males that emerge early enough to mate with early emerging females. We first observed females on 23 June, and the only two virgin

females were seen on the first and third benches on 25 June and 8 July. All females seen after 15 July had wear ratings greater than .75, indicating they were not newly emerged (Ehrlich et al., 1984). By that time inflorescences of *C. linariifolia* are usually fully opened.

As in *E. chalcedona* (Murphy, 1983; Murphy et al., 1984) *E. editha* distribution and nectar resource availability correlate: the primary source, *Senecio integerrimus*, was most abundant along the ridgetop where males were concentrated; available, although very diffusely, on benches where females were most common; and generally absent where butterflies were thinly scattered.

The hypothesis of Odendaal et al. that there should be relatively little spatial overlap between males and fertilizable females is supported by our data (Fig. 4). Detailed investigations of other populations are needed, however, since, for example, in the Jasper Ridge C demographic unit, the

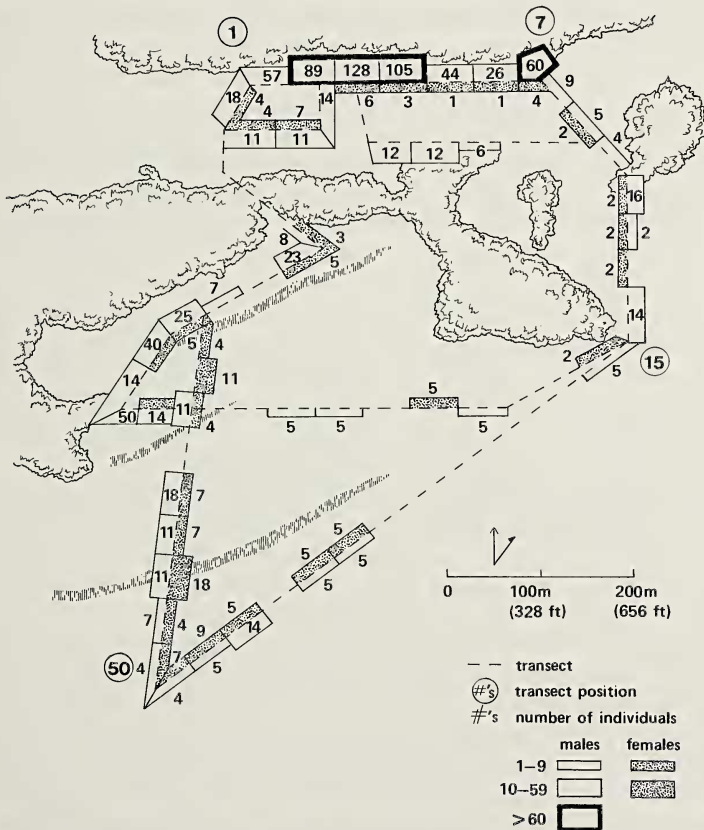


Fig. 4. Distribution of *Euphydryas editha* by sex along transect.

casual impression is that the sexes are largely co-distributed. Walking the transects at Almost Summit did not provide sufficient observation of either virgin females or matings, and assessment of the fertilizability of non-virgin females was not possible, (Labine, 1968; Ehrlich and Ehrlich, 1978). The two virgins seen were located on the first and third benches, while the matings occurred on the road, first bench and between the second and third benches. Transects were walked at a pace which may be too fast to detect teneral, flightless virgins, and were walked between 10:00 and 13:00 when virgins could be scarce if, for example, emergence were normally in the early morning or late afternoon, and most matings occurred immediately.

The choice of oviposition plant at Almont Summit is determined in part by the phenologies of the "suitable" alternatives (Holdren and Ehrlich, 1982) and it is likely that there is higher survivorship of early as compared to late egg masses, as is the case for this species at Jasper Ridge (Singer, 1972). Selection therefore might favor not only early emergence, but also prompt mating and quick oviposition on closest suitable larval host plants. Females eclosing on the benches (where males are relatively scarce) and not immediately mated there may attempt to move toward the ridgetop where mating is assured. Such movement may be discouraged by the woodland barrier separating the lower benches from the ridgetop (Fig. 1), and further delay mating and oviposition.

The proportion of males leaving the area of aggregation (rather than simply perishing there) remains to be determined. This determination may prove difficult in a population with such an open structure.

The operational sex ratio (the ratio of sexually active males to fertilizable females) at Almont Summit is clearly different in the two putative mating areas. On the ridgetop it is highly skewed toward males; on the third bench it is not. In addition, determination of the OSR must consider the variability of male sexual activity (males may emerge still sexually immature) and the fertilizability of non-virgin females.

And, of course, there remains the problem of determining exactly what prompts the male aggregation if, because of the skewed OSR, the chances of mating on the hilltop are not higher than below. The abundance of nectar is a possibility, but individuals spend much of their time perched on the road surface and flying out at passing objects.

If oviposition is preferred on the third bench and just enough males remain there to provide first and second matings, then the OSR on that bench may show a bias towards females. In this protandrous species that bias could increase over time as female emergence becomes predominant (see Iwasa et al., 1983). Thus, the suggestion of Odendaal et al. that the OSR in the mating area is heavily male-biased, may well be true for the ridgetop (if that is where most matings occur), but not for the third bench. Presumably, in both areas, the evolutionary importance of access to those

females decreases over time.

Finally, although the hypothesis that males should show little choosiness in mates was not formally tested, our observations support it. Chasing behavior is the response of male *E. editha* to moving objects, be they virgin or fertilized females, males of the same or other species, or even other flying insects, birds or shadows. Its modification into mating behavior may rest largely on the acquiescence of the butterfly pursued.

Clearly the most important data needed for rounding out the picture of mating strategies in this *E. editha* population is determination of 1) the mating success of males within and outside of the aggregation; 2) the proximate reason for the aggregation; are males attracted primarily to the nectar sources, to the warm, bare road on which they perch, to the presence of other males, or to a combination of these (or other) factors; 3) patterns of sexual activity in males, and 4) fertilizability in non-virgin females. We intend to start investigation of all of these points in the 1984 field season.

Acknowledgments. We thank Paul Buck of the Rocky Mountain Biological Laboratory for help in identifying plants, Dennis D. Murphy, and Francois A. Odendaal for reading and commenting on this manuscript, and Karen Daniels for preparing the illustrations. This work was supported in part by NSF grant DEB 82 06961.

Literature Cited

- BRUSSARD, P., 1971. Field techniques for investigations of population regulation in a "ubiquitous" butterfly. *J. Lepid. Soc.* 25:22-29.
- EHRlich, P. R. & S. E. DAVIDSON, 1960. Techniques for capture-recapture studies of Lepidoptera populations. *J. Lepid. Soc.* 14:227-229.
- _____, & A. H. EHRlich, 1978. Reproductive strategies in the butterflies: I. mating frequencies, plugging, and egg number. *J. Kansas Ent.* 51(4):666-697.
- _____, & R. R. WHITE, 1980. Colorado checkerspot butterflies: isolation, neutrality and the biospecies. *American Naturalist*, 1115(3):328-341.
- _____, A. E. LAUNER & D. D. MURPHY, 1984. Can sex ratio be defined or determined? The case of a population of checkerspot butterflies. *American Naturalist*, in press.
- HOLDREN, C. E. & P. R. EHRlich, 1982. Ecological determinants of food plant choice in the checkerspot butterfly, *Euphydryas editha* in Colorado. *Oecologia (Berl.)* 52:417-423.
- IWASA, Y., F. J. ODENDAAL, D. D. MURPHY, P. R. EHRlich & A. E. LAUNER, 1983. Emergence patterns in male butterflies: a hypothesis and a test. *Theor. Pop. Biol.* 23: 363-379.
- LABINE, P., 1968. Population biology of the butterfly, *Euphydryas editha* I. Barriers to multiple inseminations. *Evolution* 18:335-336.

- MURPHY, D. D., 1983. Nectar sources as constraints on the distribution of egg masses by the checkerspot butterfly, *Euphydryas chalcedona* (Lepidoptera: Nymphalidae). *Environmental Entomology* 12:463-466.
- , A. E. LAUNER & P. R. EHRLICH, 1983. The role of adult feeding in egg production and population dynamics of the checkerspot butterfly, *Euphydryas editha*. *Oecologia*. 56:257-263.
- , M. S. MENNINGER & P. R. EHRLICH, 1984. Nectar source distribution as a determinant of oviposition host species in *Euphydryas chalcedona*. *Oecologia* 62:269-271.
- ODENDAAL, F. A., Y. IWASA & P. R. EHRLICH, 1984. Prolonged and explosive breeding in butterflies: some preliminary comments. In press, *American Naturalist*.
- POLLARD, E., 1977. A method for assessing change in the abundance of butterflies. *Biol. Conserv.* 12:115-134.
- SINGER, M. C., 1972. Complex components of habitat suitability within a butterfly colony. *Science* 176:75-77.